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On the Significance of Neuronal Giantism in Gastropods

RHANOR GILLETTE

Department of Physiology & Biophysics and The Neuroscience Program, 524 Burrill Hall, 407 S. Goodwin Ave., University of Illinois, Urbana, Illinois 61801

Abstract. Neurons of the central ganglia of opisthobranch and pulmonate gastropods increase in size as the animals grow, some becoming veritable giants. The origins and functions of neuronal giantism are considered here from a comparative viewpoint. A review of the properties of identified neurons in a variety of opisthobranch and pulmonate species indicates that neuronal size is directly related to the extent of postsynaptic innervation. DNA endoreplication, resulting in partial or complete polyploidy, supports giantism in molluscan neurons as it does in eukaryotic cells elsewhere. Apparently, the functional significance of giantism is enhanced synthesis and transport of materials to serve an expanded presynaptic function.

Giant neurons are found in larger snails where they innervate large areas of the periphery; interneurons and sensory neurons are enlarged to a lesser degree, probably to that which enables load-matching to the peripheral effectors. Neuronal giantism may be an adaptation for the innervation of the periphery in large animals with simple behaviors and uncomplex sensoria, this adaptation enabling growth of body and CNS without a proportionate increase in neuronal number. A more complete understanding of the evolutionary and adaptive significance of neuronal giantism should be sought in comparative studies of the cellular properties of simple and complex molluscan brains.

Introduction

The condition of neuronal giantism in the pulmonate and opisthobranch gastropods has been a point of marvel at least since Buchholz' observations in 1863 (reviewed by Bullock, 1965). The conveniences offered by giant nerve cells to experimenters have also invited numerous biophysical and neuroethological studies; these have contributed greatly to our knowledge of nerve cell function and behavioral mechanisms. Even so, the significance of neuronal giants to the animals in which they are found has not been satisfactorily understood.

The question of neuronal giantism is particularly open to the methods of comparative analysis. The physiology, anatomy, and behavioral roles of giant neurons have been analyzed from a wide variety of species, and homologous neurons have been identified across species. The following paragraphs marshal evidence that supports several hypotheses for the origin and functional significance of neuronal giantism.

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The Molluscan Neuron

The typical molluscan neuron is a monopolar or bipolar cell with its soma lying in the ganglion periphery (Fig. 1). An axon enters the neuropil in the core of the ganglion where it branches off neurites that both receive and make synaptic contacts. Neurites generally sprout close to the cell body and even originate from it in opisthobranch and pulmonate neurons. Action potentials are initiated in the axon and regulated by synaptic inputs to the neurites; the region of spike initiation and synaptic activity is referred to here as the *integrating region.*

Neuronal Giantism: The Condition

The condition of "giantism" is one of degree. The central ganglia of opisthobranch and pulmonate snails commonly possess 10–20 distinct and identifiable nerve cells with cell bodies so large that they stand out from their neighbors as relative giants. Aside from the obvious giant neurons, the entire central nervous system of such animals contains only several tens of thousands of neurons, several

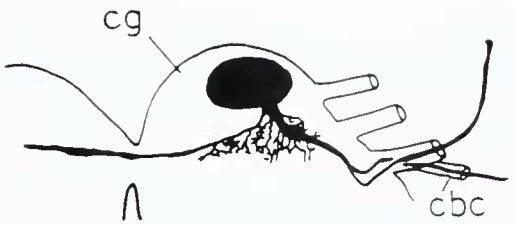

Figure 1. Typical morphology of giant neurons of pulmonates and opisthobranchs, as exemplified by this drawing of the serotonergic giant of the cerebral ganglion of *Tritonia hombergi* (from Dorsett, 1986). The large excitable soma is close to the integrating region of axon and fine neurites, where synaptic potentials occur and spikes are initiated. The large axons, with high specific membrane resistances, favor current spread from integrating region to soma.

hundred of which may be identified on the basis of position, color, synaptic and axonal connections (*cf.* Bullock, 1965; Coggeshall, 1967; Frazier *et al.*, 1967). In the larger pulmonates, the biggest neurons have somata approaching 100 μm in diameter, whereas in the larger sea slugs, certain neuronal somata reach over 700–800 μm. Moreover, as the animals increase in size, all of their identifiable neurons also grow in diameter.

Neuronal Size is Related to Postsynaptic Innervation

In approaching the nature of neuronal giantism, the first relevant observation is that neuron giants must innervate larger postsynaptic target areas than non-giants. The evidence that neuronal size is directly related to the extent of postsynaptic innervation comes from the literature characterizing a variety of identified neurons in opisthobranch and pulmonate snails. The largest neurons of the central ganglia act as effectors that innervate large areas of the periphery.

Prominent examples are a bilateral pair of giant serotonergic neurons identified in many opisthobranch and pulmonate snail species. These neurons are commonly the largest neuronal somata of the cerebral ganglion (Senseman and Gelperin, 1973; Berry and Pentreath, 1976; Weiss and Kupfermann, 1976; Gillette and Davis, 1977; Granzow and Kater, 1977). Approaching 400–500 μm in size in the larger opisthobranchs, these giant effectors send large axons down the cerebrobuccal connectives; the axons ramify within the buccal ganglion so that an axonal branch is sent out in each nerve. These axons innervate large areas of the muscular buccal mass and the esophagus; the neurons also send branches out the lip or mouth nerves of the cerebral ganglion to innervate the oral region (Fig. 2). In addition, the giant serotonergic neurons have some synaptic output in the buccal ganglia (*ibid.*).

Other well-studied giants are two of the largest neurons known, the neurons R2 and LPl1 of the anaspid opisthobranch *Aplysia californica*. R2 and LPl1 are bilaterally homologous and cholinergic, attaining soma diameters nearly 1000 μm in large animals. Due to assymetrical ganglionic fusion in the embryo, R2 is found in the abdominal ganglion, and LPl1 in the left parietal ganglion. The cell bodies give off giant axons that send branches to most ganglia and out many nerves thence innervating extensive areas of the skin (Hughes and Tauc, 1963; Cobbs and Pinsker, 1979). Their electrical activity stimulates mucus secretion (Rayport *et al.*, 1983).

Among the motorneurons innervating the gills of nudibranchs and notaspids are some of the largest neurons of the pedal, pleural, and cerebral ganglia (Blackshaw and Dorsett, 1976; Dickinson, 1979, 1980).

The well-studied buccal ganglia provide more examples of giantism. The largest neurons of opisthobranch buccal

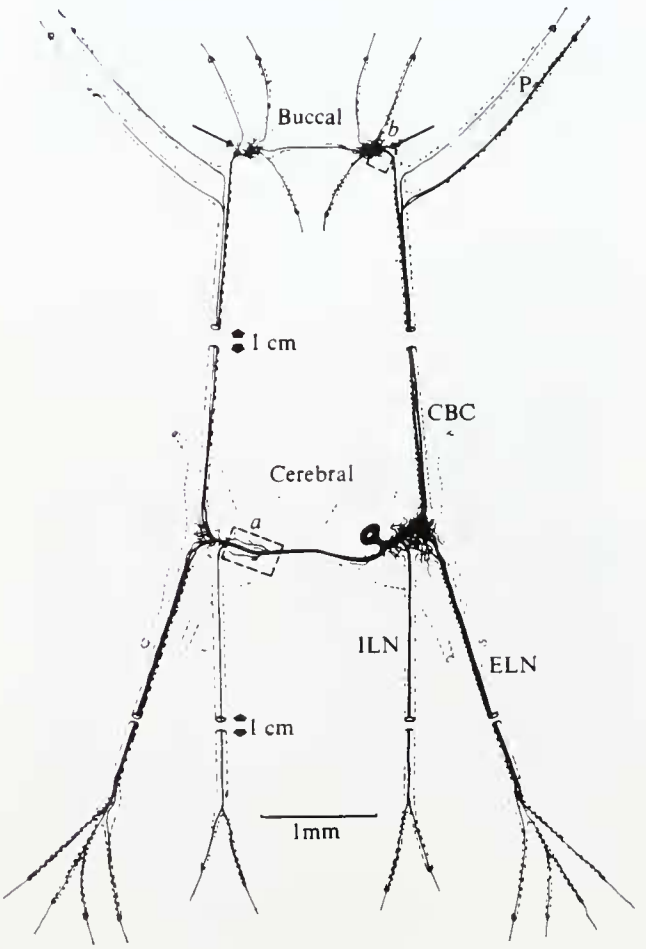

Figure 2. Extensive innervation of the periphery by the serotonergic cerebral giant neurons of *Helix pomatia* (from Berry and Pentreath, 1974). Aside from some interneuronal function in the CNS, these giants send many branches to the buccal ganglion and out the nerves to innervate the musculature of the buccal mass and esophagus. Other branches leave anterior nerves to innervate the feeding musculature of the oral region. This general plan is found in the homologous giant cells of many pulmonate and opisthobranch species.

ganglia are typically motorneurons; sensory neurons are, on the average, much smaller (Byrne *et al.*, 1974; Siegler, 1977; Spray *et al.*, 1980; Dorsett and Sigger, 1981). The largest known buccal cells may be those of the buccal ganglion of the cephalaspid *Navanax*. These neurons innervate the musculature of the large pharynx, driving its expansion during prey-capture (Spira and Bennett, 1972). In aeolid and doridacean buccal ganglia, the largest neurons are often a bilateral pair called the Dorsal White Cells (Bulloch and Dorsett, 1979). The Dorsal White Cells are peptidergic neurons that send axons out the gastroesophageal nerve to ramify over, and innervate, the large esophagus (Masinovsky and Lloyd, 1985).

Interneurons with only central synaptic outputs tend to be smaller than interneurons of dual function, *i.e.*, with both CNS output and peripheral axons innervating muscle. For instance, both the identified VWC and B31 neurons of *Pleurobranchaea* can drive intense cyclic motor output in the buccal oscillator network; but the VWC also innervates the muscular esophagus, and the diameter of its soma is nearly three times that of the B31 soma (Gillette *et al.*, 1980). Identified neurons with purely central outputs also may differ in size according to the extent of their postsynaptic output. The paired SO interneurons of the buccal ganglion of the pulmonate *Lymnaea* have a large dendritic field, and their somata are three times the size of the interneurons of the N1, N2, and N3 populations, which have collectively rather similar functions as oscillator elements, but smaller dendritic fields in the ganglion and weaker effects, individually, on the network (Elliot and Benjamin, 1985a, b).

Sensory neurons can innervate large peripheral areas, but their presynaptic function is largely confined to central ganglia, and they tend to be small. Sensory neurons of the buccal ganglia of *Pleurobranchaea* tend to have smaller somata than motorneurons innervating the same muscles of the buccal mass (Siegler, 1977). Similarly, the buccal ganglia of *Navanax* contain mechanosensory neurons that serve the pharynx and are much smaller than their postsynaptic giant motorneurons that drive the pharyngeal musculature (Spray *et al.*, 1980a, b). Sensory neurons carrying mechanosensory information from the skin of *Tritonia* are quite smaller than the interneurons and motorneurons they drive (Getting, 1977). The abdominal ganglion of *Aplysia* contains sensory neurons that innervate the gill and siphon and that are much smaller than the gill and siphon motorneurons they drive (Byrne *et al.*, 1974). In each case, the sensory neurons have smaller dendritic fields, and thus may make fewer synaptic contacts, than the larger motorneurons and interneurons.

A direct relationship between the field of postsynaptic innervation of a neuron and its soma size has been previously recognized by some workers in arthropod neurobiology. Mittenthal and Wine (1978) showed that the soma diameter of serially homologous motorneurons in the segmental nervous system of crayfish is roughly proportional to the area of the serially homologous muscle they innervate. Mellon *et al.* (1981) showed that amputation of the specialized snapping claw of the snapping shrimp *Alpheus* causes the contralateral claw and its musculature to enlarge into a larger snapping claw at subsequent molts; the soma of the claw opener motorneuron enlarges with the size of its target organ.

Finally, the peripheral effector neurons of the opisthobranch central nervous system increase in size with the growth of their target organs. The size of identified neurons, in soma diameter, axon diameter, and dendritic field, increases with the size of the animal during growth (Coggeshall, 1967; Frazier *et al.*, 1967). Accordingly, sensory interneurons monitoring the peripheral effectors and the smaller interneurons also increase in size; this is a form of load matching. All of these observations argue for a trophic relationship between the area of the innervated structure and the size of the presynaptic neuron. It is assumed here, notwithstanding the lack of direct evidence, that increases in innervated area and extent of presynaptic branching are accompanied by increases in synaptic contact area, number of synaptic sites, or both. Therefore, the beginning of the answer to the question: "Why do some neurons become giants?" is probably that their size is related to the actual total area of synaptic contact.

The Mechanism of Giantism: DNA Endoreplication

For certain cell types in many animals, an increase in cell size is generally accompanied by an increase in the actual mass of the genomic DNA and of RNA (Mirsky and Osawa, 1961; *cf.* Cavalier-Smith, 1978); this is effected either through polyploidy or polyteny. An increase in polyploidy with neuronal size has been demonstrated in molluscan neurons. The nuclei of the largest neurons of mature *Aplysia* (*e.g.*, R2) contain >0.2 μg of DNA—more than 200,000 times the haploid amount (Lasek and Dower, 1971). Neurons of the terrestrial pulmonate *Achatina*, with soma diameters of >9 μm (nuclear diameter > 7 μm), were found to be polyploid (Chase and Tolloczko, 1987). The frequency distribution of the DNA content in *Achatina* (Chase and Tollockzo, 1987) and *Planorbis* (Lombardo *et al.*, 1980) neurons indicates that endoreplication during growth probably represents selective gene amplification, rather than simple sequential doubling. However, sequential doubling may occur during growth in *Aplysia* (Coggeshall *et al.*, 1970; Lasek and Dower, 1971). Giantism in molluscan neurons is thus like giantism in other metazoan cells, and is simply based on increased amounts of nucleic acids and proteins.

Polyploid neurons of varying sizes may be common to the nervous systems of molluscs in general; *i.e.*, increasing

neuron size and ploidy may be a usual feature of growth within all of the molluscan classes; one that is, perhaps, carried to the extreme in the pulmonates and opisthobranchs.

The Functions of Giantism: Synthesis and Transport

Neuronal giants apparently innervate larger postsynaptic target areas than non-giants. Neuronal giantism, therefore, may allow an increase in animal size without a proportional increase in the number of central neurons. Giant cells in most tissues are more metabolically active than smaller cells and are frequently associated with transport and secretory processes. Familiar examples are the giant polytene cells of dipteran salivary glands, malpighian tubules, and gut, all of which are notably active in ion and peptide transport and exocytotic secretion. Thus, elaboration of DNA, RNA, and protein in many giant cells is indicative of enhanced synthetic capacity, presumably to serve the needs of increased cell activity. In giant neurons, these needs are likely to be connected with increased axon transport and secretion processes at their extensively distributed synaptic terminals.

Thus, the picture of the giant neuron becomes one where the size, synthetic capacity, and axonal transport traffic is adapted to the extent of postsynaptic innervation. The giant cells do the work of many smaller cells in other nervous systems.

The Evolutionary Origin and Integrative Significance of Neuronal Giantism in Gastropods

The occurrence of giant neurons in snails is explained in one sense by the observation that the giant neurons must innervate large postsynaptic areas. The imposing question that looms is: why do the pulmonates and opisthobranchs display such pronounced neuron giantism whereas other gastropod taxa do not? The best answer will probably rest on future comparative observations on species chosen for particular nervous system characters, but the context for such comparative observations can be set here. The approach is to enumerate the specific set of behavioral and neurophysiological characteristics that may place the opisthobranch/pulmonate line apart from other gastropods; in the process, perhaps, a few useful speculations may be generated.

Those gastropods that are distinguished by possession of a score or more of large neurons are also distinguished by the combination of the following characteristics:

1. relatively large body size;
2. motile, foraging lifestyles sustained by relatively simple behavior;
3. simple nervous systems lacking, for the most part, complex sensoria;
4. a fairly high degree of centralization within the CNS; and
5. excitable neuron cell bodies.

Although one or more of these characteristics may appear in various gastropod taxa, the appearance of all five may be relatively specific to the opisthobranch/pulmonate line.

The gastropods crept into the fossil record around 580 million years ago as minute animals 1–2 mm in shell diameter, and today most are still smaller than 5 mm. The larger modern gastropods are thus truly somatomorphic giants; their greater body size demands enhanced innervation of the periphery. In most large species, this need is met largely by an increase in brain size and neuron number; even in the opisthobranch/pulmonate line, the number of neurons (and the number of peripheral axons) increases with body size, in parallel with the striking increase in size of identified neurons (Coggeshall, 1967). But if, as has been argued, giant neurons are an adaptation for increased area of innervation, then during evolution these snails have made a trade of neuron size for neuron number in the innervation of an enlarging periphery. This trade has apparently not been made by the other larger gastropods belonging to the prosobranchs.

Large body size in gastropods is associated with a motile, foraging lifestyle, as opposed to the sedentary life of a parasite or filter feeder. Motile foragers are generally expected to exhibit a certain complexity in their behavior, complexity that would emerge from corresponding complexity in the nervous system. However, I suggest that the behavior of the opisthobranchs and pulmonates, relative to that of the larger advanced prosobranchs, is both simpler and underlain by a simpler nervous system.

CNS development is directly associated with sensory and behavioral ability. The behavior of opisthobranchs and pulmonates, like their nervous systems, probably lacks the complexity shown by the larger prosobranch snails; the number of behavioral sub-routines they use in daily living is obviously smaller than those of animals living in more complex ecological niches. Larger, more complex brains, with large numbers of small neurons, are associated with the development of sense organs for high-resolution analysis of the environment and greater complexity of behavior. In the predatory prosobranch whelks, the many tiny neurons, relatively large ganglia, and eyes are likely to mediate similarly complex behaviors. The whelk *Fusitriton oregonensis* devotes considerable behavioral strategy to reproduction. Mating pairs form seasonally and persist for as long as 4 months. Subsequently, a parent attaches its clutch of eggs to a rock surface and patrols them against predators (Eaton, 1972). Potential predators may be sensed in part by the whelk's well-developed eyes; the whelk, with twisting movements of its shell, attempts to attack and dislodge the preditor; failing that, the whelk

may directionally squirt an aversive acid secretion. The opisthobranchs and pulmonates, with their rudimentary-at-best vision and small numbers of CNS neurons, come nowhere near such complexity of behavior. Indeed, the behavior of the opisthobranchs and pulmonates really seems simple.

The relative lack of complex sensoria and their attendant complex central processing may allow the opisthobranch/pulmonate lines to live successfully with a highly reduced CNS. Their eyes are very small and quite limited in both the number and resolution of photoreceptors; in many opisthobranch species, the eyes are even internalized. Their function may be largely limited to setting the circadian rhythms of animal activity (Jacklet, 1969). High resolution eyes in the cephalopods are associated with comparably high resolution, visually directed motor behavior (*cf.*, Wells, 1978). High resolution in sensory-motor systems requires larger numbers of neurons, as are found in the cephalopod optic lobes. The opisthobranchs get along mostly with the environmental information provided by chemosensory and tactile abilities. The opisthobranchs and pulmonates do have specialized chemosensory sites for detecting food: the rhinophores, and the tentacles and other regions about the oral area. These sites appear to be served by peripheral ganglia that may take the burden of a great deal of sensory-motor processing (*cf.*, Mpitsos and Lukowiak, 1986), leaving the central nervous system to process simple tactile information and to integrate motivational and learning processes with the expression of behavior.

Contrasting examples support this interpretation. Some pulmonates and prosobranchs have developed accessory CNS ganglionic lobes; these structures are associated with chemosensation and are composed of many smaller neurons (*cf.*, Bullock, 1965; Chase and Tolloczko, 1989). In the terrestrial slug *Limax*, the structure is the procerebral lobe, and it shows oscillating electrical field potentials characteristic of rather complex sensory feature extraction systems in vertebrates (Gelperin and Tank, 1990). Outside of the gastropods, the obvious example is the complexity of sensoria and sensory processing in the complex brains of cephalopods. In the opisthobranchs and pulmonates, the lack of complexity in sensoria and underlying neural processing underscores their simplicity of brain and lifestyle.

Finally, the opisthobranch and pulmonate nervous systems show a relatively high degree of centralization into a few discrete ganglia. Although centralization and cephalization have not proceeded as far as in the cephalopods, these characteristics still distinguish them from the mostly sessile bivalves and the parasitic or filter-feeding gastropods that rely heavily on peripheral control of reflexes and show generally less centralization. It also distinguishes them from large, motile mollusks like the giant chitons, from which giant neurons are not reported. The chitons attain large size in some cases, and are slowly motile, but their nervous system is only poorly centralized relative to that of the opisthobranchs and pulmonates. Amphineuran ganglia are simply formed nodes lying on a major nerve ring, and many neuronal somata are simply dispersed along the nerves and connectives in a primitive medullary condition (*cf.*, Bullock, 1965).

Thus, snails with giant neurons constitute a group that has grown large in body size, but has retained an uncomplicated behavioral repertory and sensory-motor capacities. To serve the innervation needs of the enlarged body, the nervous system has favored an increase in neuron size relative to neuron number.

The above characters provide the context within which I think we must seek the evolutionary reasons that some snails chose the architecture of neuronal giantism in their nervous systems. Why didn't they choose instead to innervate their enlarged periphery with many smaller central neurons, like their large prosobranch cousins? The developmental simplicity of innervating a large area with one neuron rather than many may be a useful consideration. Another is that neuronal giantism allows increased animal size without a proportional increase in central neuron number.

A potential answer lies in the electrophysiological properties of neurons of simple and complex gastropod brains. In molluscan ganglia, the neurons lie peripherally and send axons into a central neuropil to make synaptic connections. For the opisthobranch and pulmonate snails the neuronal somata are excitable and are placed spatially and electrically quite close to the integrating region (Gorman and Mirolli, 1972; Graubard, 1975); they are thus able to follow almost synchronously the spike activity of the integrating region (*cf.*, Fig. 1). In larger ganglia, the distances from the synaptic integrating region in the neuropil, where spikes are initiated, to soma also become longer. Thus, for a neuron that grows in pace with the whole ganglion, the larger axon diameter would enhance the synchrony of soma and integrating region. In this manner, the continuing enlargement of neuronal somata with the growth of the organism may not only adapt the cells to the innervation of an enlarged periphery, but also to an increased separation of the soma from the integrating region.

Some data suggest that the very small neuronal somata of advanced cephalopod ganglia are inexcitable (Gilly and Brismar, 1989; Williamson and Budelmann, 1991; Robertson *et al.*, 1990), like those of arthropods. Many of these somata lie rather distant from the neuropil integrating regions, because they are packed on top of many intervening cells in the cell body layer (*cf.*, Young, 1971). For a small neuron, this longer distance could cause a disadvantageous desynchronization of the action potential

currents between the soma and integrating region, with the result that the late somatic currents would interfere with ongoing integration (in the worst case, by reflecting spikes). Thus, for the nervous systems having a high proportion of such small neurons, it might be functionally advantageous if the cellular mechanisms of somatic excitability were turned off. We would then wonder, in general, whether large brains with many small neurons have inexcitable somata. Do gastropods, such as the larger whelks with large central ganglia and many small neuron somata distant from the integrating neuropil, have spiking or non-spiking somata? Few intracellular recordings have been made in the complex nervous systems of the advanced giant prosobranchs, but if their small neuron somata were also inexcitable, a strong case could be made that the simplicity and small neuronal numbers of the opisthobranch/pulmonate central nervous system permits the retention, in evolution, of excitable somata with an increase in the size of ganglia.

Conclusion

The opisthobranch and pulmonate gastropods constitute large and successful taxa. In the picture drawn here, selection during evolution has tightly interwoven neuronal giantism in the CNS with the physiology and behavior of the animal. A number of testable hypotheses have been proposed, and each can be verified or falsified by more detailed, quantitative observations. The hoped-for result, a more complete resolution of the adaptive significance of neuronal giantism, may one day make a useful contribution to our understanding of how the nervous system has evolved in tandem with behavior.

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